

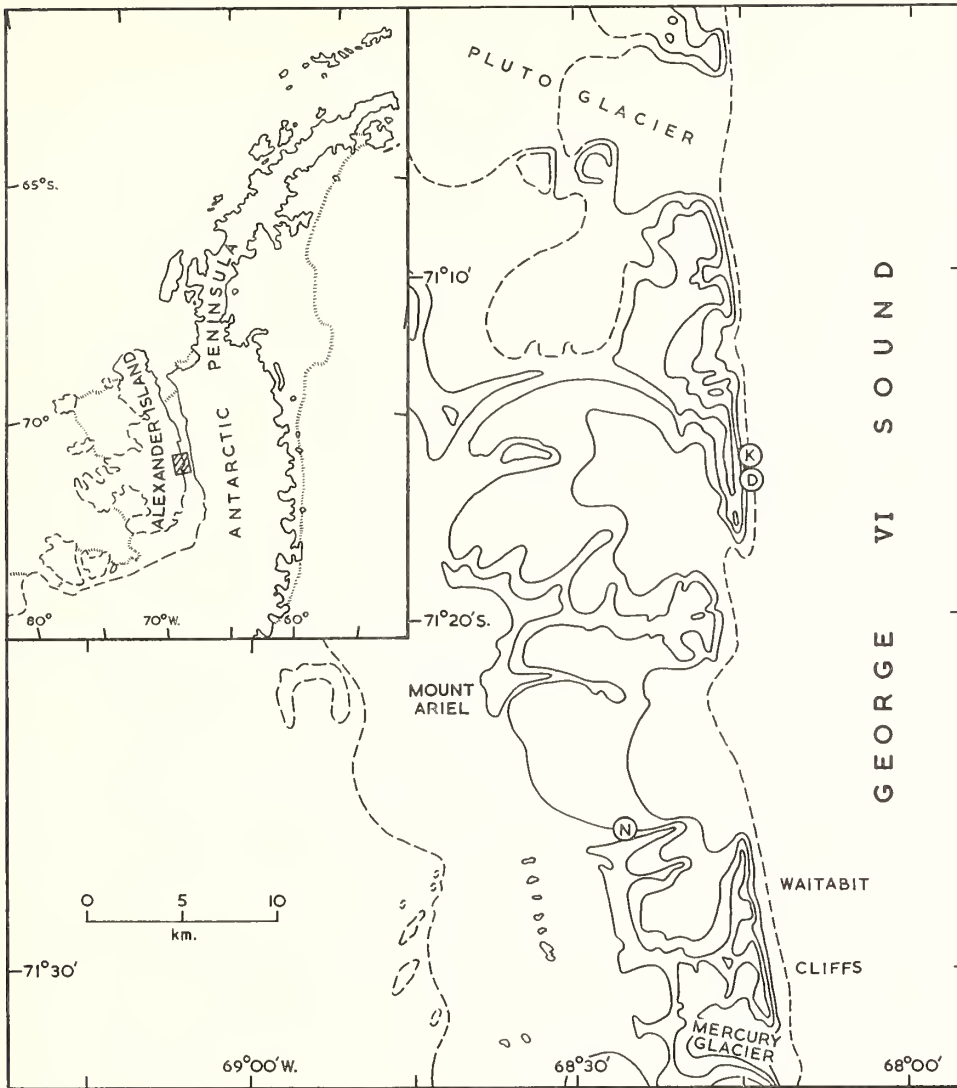
THALLOPHYTE BORINGS IN PHOSPHATIC FOSSILS FROM THE LOWER CRETACEOUS OF SOUTH-EAST ALEXANDER ISLAND, ANTARCTICA

by BRIAN J. TAYLOR

ABSTRACT. Numerous unbranched fungal borings penetrate the phosphatic cuticles and shells of decapods and discinid brachiopods from the Lower Cretaceous (? Upper Neocomian–Upper Aptian) of south-east Alexander Island, Antarctica. Comparable borings probably made by a similar saprotrophic, endogenous, and host-specific fungus occur in other phosphatic fossils in the geological record. A high host specificity is particularly characteristic of aquatic phycomycetous zoospores, many of which are chitinophilic. Spherules of iron pyrites and hydrated iron oxide at the blind ends of many of the borings were probably deposited in a suitable micro-environment generated by a decaying part of the thallophyte.

IN the Lower Cretaceous sedimentary succession exposed in south-east Alexander Island (lat. 71° S., long. 70° W.), Antarctica, between Pluto and Mercury Glaciers (lat. 71° 07' to 71° 34' S.), macrurous decapods and discinid brachiopods are quite common, particularly at certain localities. Although most of the specimens are natural moulds, a few have black or more commonly bluish white shells. From amongst the latter, five decapods and two discinids were examined by means of thin sections and cellulose peels. Additional specimens studied by X-ray diffraction indicate that the fossil decapod cuticles and the shells of *Discinisca variabilis* Thomson are composed of either calcium phosphate or hydroxyapatite and that both are practically identical in composition with modern *Lingula*. The composition and micro-structure of the fossil decapod cuticles will be described elsewhere.

The five decapod specimens, comprising four species from at least three different horizons, were found in dark indurated mudstones at the northern end of Waitabit Cliffs and three other localities (D, K, and N) in south-east Alexander Island (text-fig. 1). Three of the species, *Glyphea alexandri* Taylor, *Palaeastacus foersteri* Taylor, and *Palaeastacus* cf. *sussexiensis* Mantell are represented by almost complete carapaces, whereas the fourth consists of only a glypheid cheliped. The cheliped is preserved in a concretion. The cuticles of the articulated specimens and small areas of the cheliped cuticle (all remarkably well preserved) contain numerous tubiform borings which are not visible in the hand specimen. Practically identical borings also occur in two discinid shells from Mount Ariel and the northern part of Waitabit Cliffs. The similarity of the borings in size and general morphology throughout all the affected shell and cuticular fragments suggest that they were probably made by the same type of organism. The borings are best developed in the thicker parts of the cuticle and are rare only in the cheliped, which may have been effectively protected by the syngenetic formation of the concretion. Most of the other decapods and discinids in the succession were probably affected by the same 'mycosis'.



TEXT-FIG. 1. Map of part of south-east Alexander Island showing localities where bored decapods and discinid brachiopods were collected. Inset: location of field area (cross-hatched) in relation to Alexander Island and Antarctic Peninsula.

GENERAL MORPHOLOGY

The borings, which are vermiform, occur as straight, filiform, or sigmoidal tubules, planicurves, planispirals or as open sinistral and dextral helices comprising 4–7 coils (Pl. 52). They are circular in cross-section, of constant diameter, aseptate, and frequently intertwined. In both ordinary light and under crossed nicols, the white or pale brown borings contrast with the darker amber of the cuticle. With one possible exception (in

specimen KG.3.56 of *Discinisca variabilis*), the tubules are unbranched, although branching is frequently simulated by intersections, coalescence, or by tubules passing over or under one another. Thin dark margins defining the boundaries of the tubules (Pl. 52) may either represent walls deposited by the boring organism or Becke effects.

Many of the blind ends of the borings terminate in a round or bullet-shaped granule of iron pyrites or hydrated pyrites which is black or red in colour (Pl. 52, figs. 2, 3, 5, 7). Most of the red forms are translucent. Although these spherules are relatively common in the matrix, they appear to be concentrated either around the outside of the decapods or they fill voids in the cuticle. Spherules in the tubules other than those at the blind ends invariably represent the junction of intersecting borings.

The normal diameter size range of the tubules is 3–15 μm . However, exceptionally fine borings 0.60 μm wide and much larger tubules of 30–50 μm occur. The pyrite granules at the blind ends of the latter are aggregated. Small tubules within larger ones probably represent more than one period of 'infestation'. Most of the tubules are perpendicular or oblique to the cuticular surface and many extend across the whole of the procuticle and the epicuticle where the latter is preserved. Several are deflected on approaching the inner or outer margin (Pl. 52, fig. 1).

Where the tubules are in clusters or sheaves resembling fibrous tumours (Pl. 52, fig. 3; Pl. 53, fig. 1), the cuticle has almost been completely removed or assimilated. The location of these tumour-like developments, which seem to represent centres of proliferation, appears to be haphazard. There are no indications that the boring organism utilized any microstructural feature of the decapod cuticle, such as the lamellae or pore-canal fibrils. Although many of the tubules appear to be empty, some are filled with an as yet unidentified mineral.

In general, the tubules in the decapod cuticles and discinid shells cannot be traced into the surrounding matrix. However, in several of the decapod thin sections, a few tubules seem to lie fractionally outside the cuticle, and in one specimen there appears to be a small area of completely dissociated tubules. Unfortunately, in the absence of any colour contrast such as in the decapod cuticles, it is difficult to detect tubules in the matrices.

By comparison, the borings in the two discinids examined in thin section are poorly developed. The shells are much thinner (120 μm compared with 480 μm) and one of them (KG.3.56) is fragmentary. In the better-preserved specimen (KG.103.81), the outer, colourless cross-fibred layer is not bored but the thicker inner layer (which is brown in colour and sub-horizontally laminated) contains several small borings 0.6–4.5 μm in diameter, some of which terminate in a particle of iron pyrites.

PRESERVATION AND SEDIMENTARY ENVIRONMENT OF THE BORED DECAPODS AND DISCINIDS

The bored decapods and discinids probably lived and died within the photic zone (living *Discinisca* commonly occurs in less than 16.5 m (Stenzel 1965; Thomson, in press). The almost complete preservation of many of the decapods and of other articulated fossils in the same succession (ophiuroids and stemmed crinoids), the rarity of epizoans, and the frequent occurrence of burrowing bivalves in life positions suggest quiet, non-turbulent conditions occasionally coupled with rapid sedimentation. There were few

scavengers. At one locality (K), the decapods may have lived and died in the lee of an offshore bar where abnormally large amounts of plant debris and bored wood fragments accumulated.

On the assumption that the borer was not completely heterotrophic and that the decapod cuticles were secondarily phosphatized in a way analogous to that reported from the Pacific Ocean (Goldberg and Parker 1960), it is probable that the dead decapods or their exuviae and the discinids lay uncovered long enough for the former to be recrystallized and for the spores of some thallopiphyte to settle and proliferate.

Although the seawater probably had a normal pH value, the non-occurrence in Alexander Island of bedded limestones (other than calcareous concretions) and the large amounts of disseminated and nodular iron pyrites suggest that toxic conditions may have existed below the water/sediment interface. The occurrence of *Lingula*, which can tolerate such conditions, and the phosphatization of the decapod cuticles support this view. The associated fossil flora suggests that the climate was humid and temperate. The sea temperatures may also have been relatively warm since *Trigonia*, which occurs at localities K and D in the same strata as the decapods, is today restricted to the warm waters around Australia (Arkell 1956, p. 616). Deltaic or fluviatile conditions may also have existed periodically.

DISCUSSION

The vermiform tubules in the decapods and discinids are too small and complex for solution cavities. Similarly, because of the high host specificity of the tubules and their absence in the matrices and more richly pyritized shells at the same localities, they are unlikely to have been formed inorganically by 'ambient' pyrites (Tyler and Barghoorn 1963). Therefore, it seems probable that the tubules represent the borings of a microscopic organism.

Like most other trace fossils, fossil borings (particularly the tubiform type) are difficult to interpret. Different organisms with similar habits frequently produce practically identical borings, whereas the same organism penetrating various substrata for one or more purposes (shelter, nutrition, or anchorage) may produce a number of dissimilar cavities. [Here, *substratum* refers to the medium penetrated by the boring organism and *substrate* the chemical compound acted upon by the borer's enzymes.] With some notable exceptions, few fossil borings are morphologically diagnostic and the body fossils are rarely preserved. However, if particular borings can only be grouped in the broadest sense (as Algae, Fungi, or Bacteria), they may contribute towards an understanding of the sedimentary environment in which the host lived or was buried.

The type of vermiform boring discussed here has not previously been recorded in fossil decapod cuticles. However, similar borings are known from the Precambrian (Gruner 1923; Tyler and Barghoorn 1963) and from several Palaeozoic fossils. Occasionally, living lower plants penetrating mainly calcareous substrata produce borings which are comparable in their general morphology (Peyer 1945, fig. 19, p. 515; Schmidt 1962, fig. 2a, p. 247). Because the Antarctic borings are better developed in the decapods than in *Discinisca variabilis*, the following comments are concerned mainly with their occurrence in the arthropods.

Although certain Sporozoa, Ciliophora, Cestoda, and Copepoda are parasitic or

symbiotic on decapods, they only inhabit living or dead soft tissues and do not penetrate the cuticle. Similarly, because of their small size, the vermiform tubules are unlikely to have been made by boring trematodes, annelids, bryozoans, cirripedes, and most sponges, the cavities of which are commonly macroscopic. Although the tumour-like growth of *Sacculina* and *Thompsonia* (two parasitic cirripedes) are similar to the bunched tubules in the decapods, the cirripedes only produce a straight hole in the decapod cuticle and the rhizoidal systems are restricted to the soft parts (Borradaile *et al.* 1959). Despite their dubious nature, the origin of the vermiform tubules can be discussed in terms of four groups of parasitic or saprotrophic thallophytes, i.e. Actinomycetes, Bacteria, Algae, and Fungi.

Although the Actinomycetes (which occupy a position between the filamentous Fungi and the true Bacteria) are much smaller than the tubules and are usually branched (Waksman 1959, p. 71), there is at least a superficial resemblance between the coiled sporogenous hyphae of some Actinomycetes and the helical tubules. Moreover, the Actinomycetes attack chitin by secreting chitinase and, more than any other group of micro-organism, they are particularly active at decomposing proteins which they convert to amino acids and ammonia (Waksman 1959). However, the borings are too wide for Actinomycetes (*pers. comm.*, H. Lechevalier), and for Bacteria which are usually less than 2 μm in diameter.

Although parasitic or saprotrophic Fungi on arthropods (usually entomophilous forms) can pierce through unbroken cuticle from the outside and are both chitinivorous (e.g. Laboulbeniaceae) and pathogenic, they penetrate the cuticle only to reach the host's soft parts where the hyphae proliferate (Atkins 1929, 1954; Lefebvre 1934; Takahashi 1958). Nevertheless, the hyphae of the many-branched *Leptolegnia marina*, which bores through the cuticle and soft tissues of live pea-crabs, are approximately the same order of size as the vermiform tubules.

Because many living boring Algae and Fungi are similar morphologically and have comparable pH ranges and size ranges (fungal and algal borings with diameters between 4 and 30 μm overlap one another), the affinities of several fossil forms are uncertain or disputed (Seward 1898; Pia 1927). However, observations based on the morphology, substrate, specificity, and palaeobathymetry may indicate a likely origin for a particular type of boring.

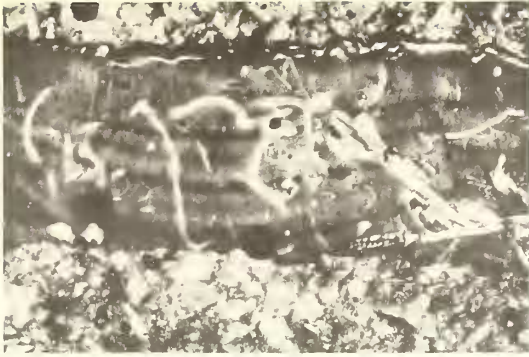
From amongst the many occurrences of essentially unbranched fossil 'algal' and

EXPLANATION OF PLATE 52

Figs. 1-8. Thin sections through parts of the cuticle of a specimen of *Glyphea alexandri* Taylor (KG.18.43) showing numerous borings attributed to a saprotrophic fungus. The sections are shown in ordinary light and all but one (Fig. 8) are approximately normal to the cuticular surface. 1, (slide KG.18.43a), $\times 90$. 2, (KG.18.43a), $\times 230$. 3, (KG.18.43a), $\times 240$. 4, (KG.18.43e), $\times 230$. 5, (KG.18.43e), $\times 270$. 6, (KG.18.43b), $\times 230$. 7, (KG.18.43e), $\times 230$. 8, (KG.18.43f), $\times 1000$.

EXPLANATION OF PLATE 53

Figs. 1-3. Thin sections through the cuticle of *Gl. alexandri* Taylor (specimen KG.18.43) showing borings attributed to a saprotrophic fungus. 1, (slide KG.18.43a), $\times 420$. 2, (KG.18.43b), $\times 300$ and in X-nicols. 3, (KG.18.43c), $\times 300$; the cuticle in the right-hand corner in fig. 3 has been virtually assimilated by the boring organism. 4, 5, 'Vermiform tubules' in the cuticle of *Ceratiocaris papilio* Salter (slide 291, carapace 1), both $\times 300$. Figs. 4, 5, by kind permission of Dr. W. D. I. Rolfe.



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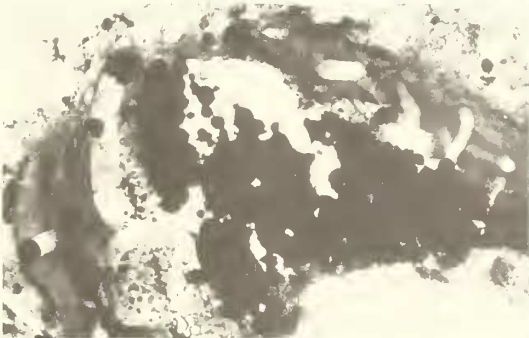
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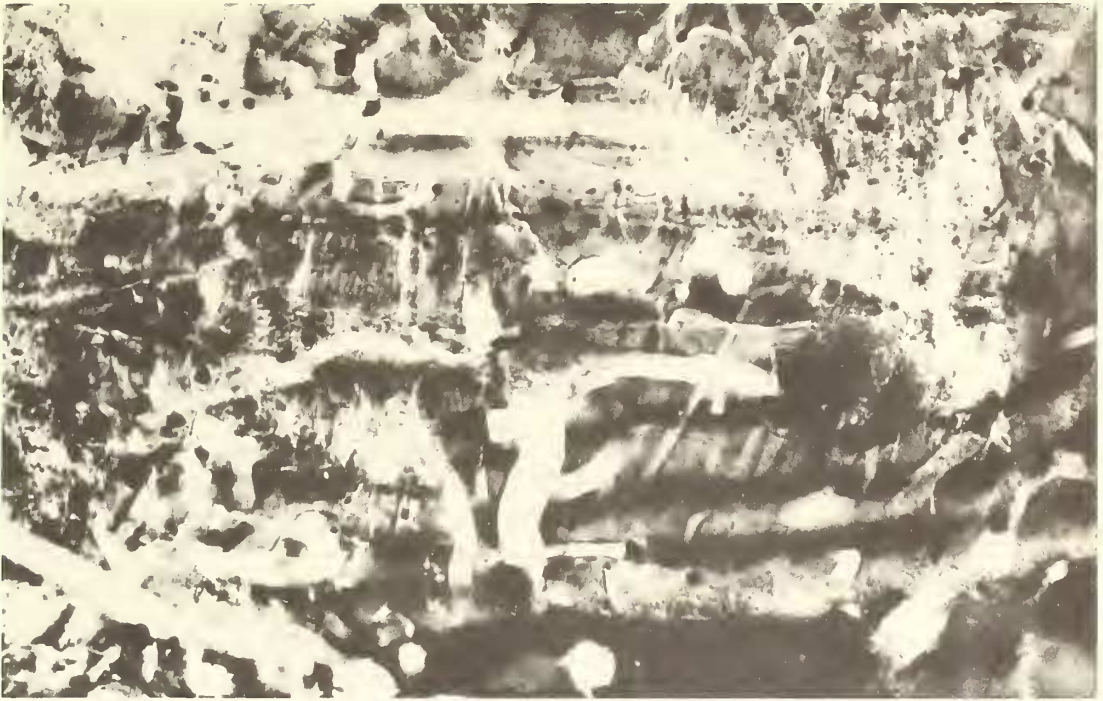
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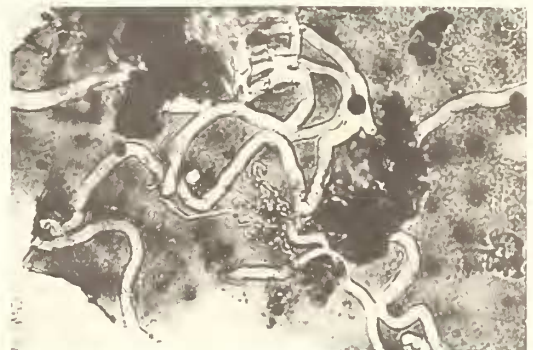
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